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A new species of *Mindomys* (Rodentia, Cricetidae) with remarks on external traits as indicators of arboreality in sigmodontine rodents

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Abstract

The diversity of the oryzomyine rat *Mindomys* (Cricetidae, Sigmodontinae, Oryzomyini), is doubled here with the description of a new species from the remote Cordillera de Kutukú (Ecuador). The novel form can be easily differentiated from *Mindomys hammondi* –type species of the genus– by a large set of anatomical traits including, among others, larger jugals, parietal "wings" extending to zygomatic roots, larger otic capsules, well-exposed petrosals, narrow zygomatic plates almost without upper free borders, foramen magnum caudally oriented, larger molars, and accessory root of first upper molar present. Until now, the records of *Mindomys* were restricted to western Andean foothills. The material from Kutukú highlights an Amazonian species and reinforces the valuable biological significance of isolated mountain ranges in eastern Ecuador. Since *Mindomys* shows some external traits classically related to arboreal life, here we present a brief reappraisal of this poorly explored topic. A partially neglected anatomical system in sigmodontine studies, the fore feet, encloses crucial information reflecting arboreality.

Key Words

Arboreal cricetids, Ecuador, fore feet, Kutukú mountain range, Oryzomyini, Sigmodontinae

Introduction

Arboreality, the adaptation for moving or living in trees, is rare in the sigmodontine universe (about 10% over 450 living species). This is striking because forests cover a substantial portion of South and Middle America, which are the subcontinents where the subfamily made its main radiation (Patton et al. 2015; Pardiñas et al. 2017). A handful of members of a few tribes show morphological features traditionally associated with arboreal life, although rarely tested (Maestri et al. 2017; Camargo et al. 2019). Much of this diversity is concentrated into a single group, the Oryzomyini, which is the most species-rich and widespread clade in the subfamily (Weksler 2006; Brito et al. 2020).

Among the supposedly arboreal oryzomyines is a large rat, *Mindomys* Weksler, Percequillo & Voss, 2006. Its type-species and until now single representative, *Mindomys hammondi* (Thomas, 1913) is known from a few specimens, all collected in the Andean foothill forests of northwestern Ecuador. Information about *Mindomys* is mostly restricted to basic morphological and geographical data (Hershkovitz 1970; Weksler et al. 2006; Percequillo 2015b; Brito et al. 2021).

After three expeditions to the almost inaccessible Cordillera de Kutukú, an isolated mountain range in southeastern Ecuador, we collected a single adult male of a large oryzomyine rat. Comparisons with all recorded Ecuadorian members of the tribe revealed similarities with *M. hammondi*. Here we describe the animal from Kutukú

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as a new species of *Mindomys*, adding by this action not solely the first Amazonian taxon for the genus but also valuable information on external anatomy. The latter reinforces the association of these rats with arboreal life.

Materials and methods

Studied specimens

The holotype of the new species (see below) was collected in Cordillera de Kutukú during a field trip carried out by JB. These sampling trips involved a cumulative trap effort of 1,200 trap-nights. Capture, handling, and preservation of specimens captured in the field, followed guidelines established by the American Association of Mammalogists (Sikes et al. 2016). The specimen was preserved as a dry skin and skeleton plus tissues. It was compared to the holotype of *Mindomys hammondi* accessed through a 3D-model of its skull purchased from the Natural History Museum (**NHMUK**; London, United Kingdom), plus several digital pictures of the same specimen. Also, we employed numerous photographs of unstudied specimens referred to *M. hammondi* and housed in the Göteborg Naturhistoriska Musset (Gothenburg, Sweden). These individuals were obtained (probably purchased from local collectors; see Voss 1988) by Ludovic Söderström during the 1920s and identified by Tirira and Högström (2011). Additional information about *M. hammondi* was retrieved from literature (Thomas 1913; Weksler et al. 2006; Percequillo 2015b) as well as a recently secured specimen from the Ecuadorian Reserva Drácula (Brito et al. 2021). The animal from Kutukú was directly compared to numerous other oryzomyines belonging to the Ecuadorian mammal collections of Museo de la Escuela Politécnica Nacional (**MEPN**; Quito) and Instituto Nacional de Biodiversidad INABIO (**MECN**; also known as Museo Ecuatoriano de Ciencias Naturales, Quito). All studied material, included those used in comparisons and illustrations, is listed in Appendix 1.

Data collection: anatomy and measurements

Craniodental anatomy was described according to the main concepts explained in Carleton and Musser (1989); molar occlusal morphology was addressed following the topographical approach of Reig (1977; upper and lower molars are identified as M/m, respectively). Metrical descriptors employed to characterize the holotype of the new form described here are standard external and craniodental measurements. The latter, expressed in millimeters (mm), were obtained with digital calipers and are those described by Musser et al. (1998).

For more detailed scrutiny, including access to internal structures without damage, the skull of the holotype of the new species described here was scanned by using a high-resolution micro-computed tomography (micro-CT) desktop device (Bruker SkyScan 1173, Kontenich, Belgium) at the Zoologisches Forschungsmuseum Alexander Koenig (**ZFMK**, Bonn, Germany). To avoid movements during scanning, the material was placed in a small plastic container embedded in cotton wool. Acquisition parameters comprised: an X-ray beam (source voltage 43 kV and current 114 µA) without the use of a filter; 1,200 projections of 500 ms exposure time each with a frame averaging of 5 recorded over a 360° continuous rotation, resulting in a scan duration of 1 h 13 min; a magnification setup generating data with an isotropic voxel size of 17.03 µm. The CT-dataset was reconstructed with N-Recon software (Bruker MicroCT, Kontich, Belgium) and rendered in three dimensions using CTVox for Windows 64 bits version 2.6 (Bruker MicroCT, Kontich, Belgium). For comparison, the holotype of *M. hammondi* (NHMUK 13.10.24.58) was scanned at the Imaging Analysis Centre of the NHMUK using a Nikon Metrology HMX ST 225 (Nikon, Tring, UK). Acquisition parameters comprised: an X-ray beam (source voltage 100 kV and current 150 µA) filtered with 0.1 mm of copper; 3142 projections of 500 ms exposure time each with a frame averaging of 2 recorded over a 360° continuous rotation; a magnification setup generating data with an isotropic voxel size of 22.67 µm. A filtered back projection algorithm was used for the tomographic reconstruction, using the CT-agent software (Nikon Metrology GmbH, Alzenau, Germany), producing a 16-bit uncompressed raw volume. Finally, this dataset was rendered in three dimensions with Amira software (Thermo Fisher Scientific, Hillsboro, USA).

Molecular techniques

DNA was extracted from a sample of muscle of the studied specimen preserved in ethanol 90% using the extraction protocol detailed in Bilton and Jaarola (1996). Amplification of the mitochondrial cytochrome b (*Cyt b*) gene employing the primers MVZ05 and MVZ16H, with the thermal profile described in Smith and Patton (1993). The analyzed sequences data matrix also included sequences of an additional *Mindomys hammondi* collected in Reserva Drácula (Brito et al. 2021) and of the genus *Pattonimus* (Brito et al. 2020); in total the matrix included 23 of 29 described Oryzomyini genera (Pardiñas et al. 2017; Brito et al. 2020). Sequences were edited in Geneious R.11.5 (https://www.geneious.com), and aligned with the CLUSTALW tool. All sequences employed in the phylogenetic analyses are provided in (Suppl. material 1).

Phylogenetic analyses

Genetic data were analyzed using maximum likelihood (ML) and Bayesian inference (BI). The analysis was conducted with MrBayes v.3.2 (Ronquist et al. 2012) under the model GTR + G + I. Four Markov chains were run twice for 10 million generations (sampled every 1,000).

The first 25% of sampled trees were discarded as "burn-in," and the remaining trees were used to compute a 50% majority rule consensus tree. Convergence was evaluated by the effective sample size (ESS ≥ 100), and the potential scale reduction factor was also verified (PSRF = 1). The ML analysis was conducted with RAxMLv8.2.10 (Stamatakis 2014) under the GTRGAMMA model, with 10 alternative runs on randomized maximum parsimony starting trees. Nodal support (BS) was assessed with the rapid bootstrapping algorithm under the MRE-based bootstrapping criterion (100 replicates). Genetic distances (p – distance) were calculated using the software MEGA X (Kumar et al. 2018).

Results

A combination of external (e.g., absence of anus promontory) and craniodental traits (e.g., absence of suspensory process of the squamosal overlapped to the tegmen tympani) plus the overall appearance of the cranium and molars firmly indicate that the specimen collected in the Cordillera de Kutukú (MECN 5809) is an oryzomyine (Weksler 2006). Therefore, the morphological scrutiny was focused on the members of this tribe represented in Ecuadorian montane forests, selecting those showing a combination of large body size, long tail, small ears, and brachydont tubercular complex molars. This pointed to the genera *Euryoryzomys*, *Mindomys*, *Nephelomys*, and *Tanyuromys*. Fortunately, almost all these forms have been revised, at least at generic level (e.g., Weksler et al. 2006; McCain et al. 2007; Pine et al. 2012; Carleton and Musser 2015; Tinoco 2015; Prado and Percequillo 2018; Timm et al. 2018; Brito et al. 2021; Ruelas et al. 2021). The animal from Kutukú was included in an extensive database constructed using those characters selected in the original generic diagnosis, with the purpose in search of generic assignment (Supp. material 2). Three other oryzomyine genera, which also occur in Ecuadorian montane forests, including a species-rich one (*Oecomys*) and an apparently monotypic one (*Sigmodontomys*), were primarily excluded by evident differences in molar morphology (Figs 1, 2). *Oecomys*, mostly composed of small or medium-sized forms (Carleton and Musser 2015), has comparatively small brachydont, but moderately simplified molars. *Sigmodontomys*, in contrast, is a poorly-known medium-sized oryzomyine (Weksler 2015a), with an obvious tendency towards molar lophodonty. The latter is also true for the recently described *Pattonimus* (Brito et al. 2020).

These comparisons, carried out at a generic level, led us to a confident working hypothesis that the Kutukú specimen represents a new species of *Mindomys*. Summarized results based on those anatomical traits selected to describe several oryzomyine genera (Weksler et al. 2006: tables 2 and 3) are presented in Table 1. Accordingly, the specimen from Kutukú is difficult to classify among *Euryoryzomys*, as it has important external (e.g., small ear, very long vibrissae, unicolored tail) and craniodental (e.g., large jugal, capsular process absent, long m2 hypoflexus) differences. With respect to *Nephelomys*, the different characteristics presented by members of this genus (e.g., short vibrissae, long incisive foramina, one internal fossette in M2) suggest that the material under study cannot be allocated there either. *Tanyuromys*, for which a new species with Ecuadorian populations has recently been added (Timm et

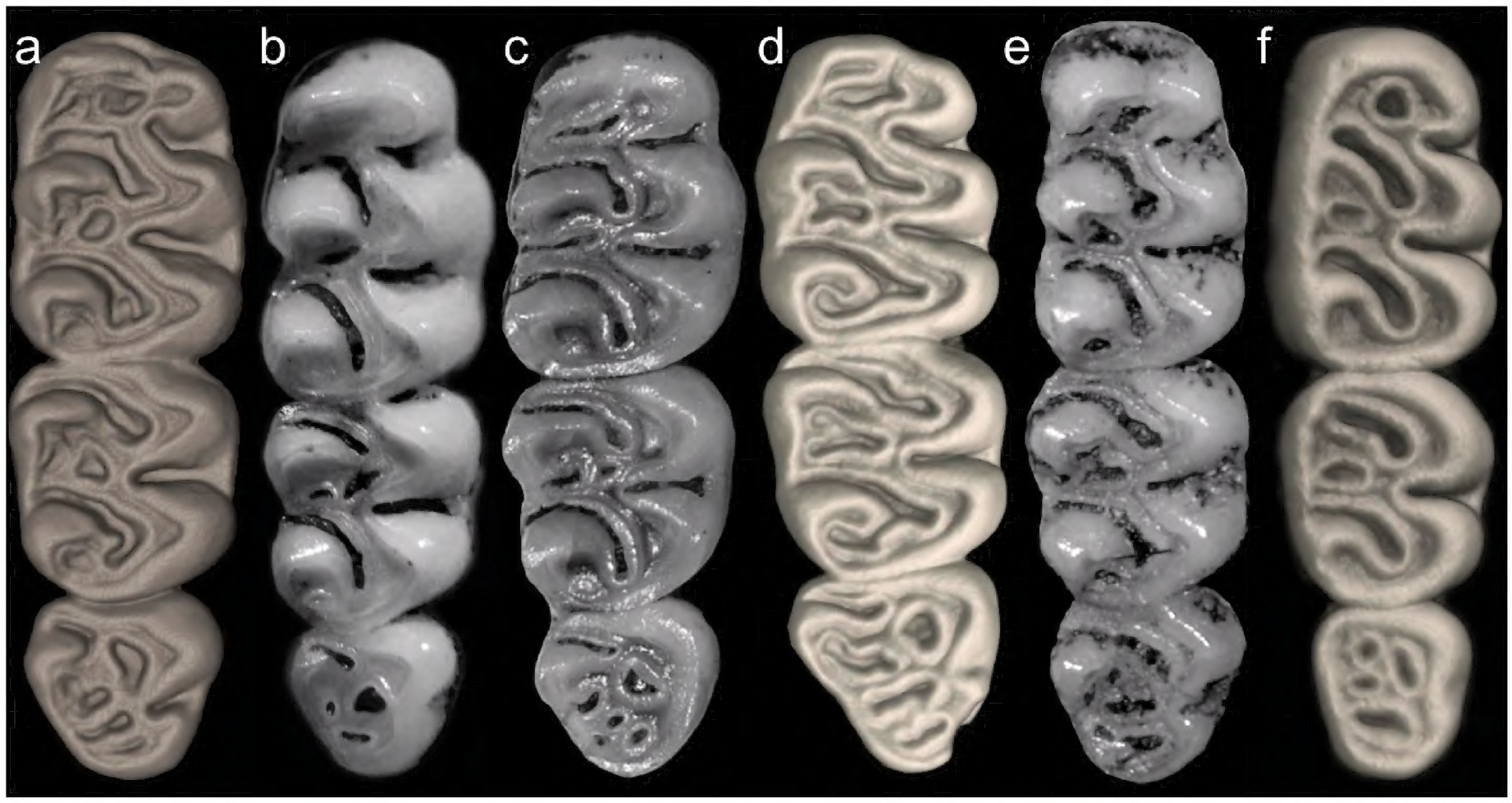

Figure 1. Occlusal views of right upper toothrows in several oryzomyines which inhabit Ecuadorian montane forests: *Mindomys* sp. nov. (**a** MECN 5809), *Euryoryzomys macconnelli* (**b** MUSM 27054), *Nephelomys auriventer* (**c** MECN 3797), *Tanyuromys thomasleei* (**d** MECN 3407), *Oecomys superans* (**e** MECN 3371), and *Sigmodontomys alfari* (**f** MECN 6021). Figures are not to scale to facilitate comparisons.

Figure 2. Occlusal views of right lower toothrows in several oryzomyines which inhabit Ecuadorian montane forests: *Mindomys* sp. nov. (**a** MECN 5809), *Euryoryzomys macconnelli* (**b** MUSM 27054), *Nephelomys auriventer* (**c** MECN 3797), *Tanyuromys thomasleei* (**d** MECN 3407), *Oecomys superans* (**e** MECN 3371), and *Sigmodontomys alfari* (**f** MECN 6021). Figures are not to scale to facilitate comparisons.

Table 1. Selected morphological comparisons between the specimen collected in Kutukú (Ecuador) and similar oryzomyine genera.

	Kutukú specimen	***Mindomys*[1]**	***Pattonimus*[2]**	***Euryoryzomys*[3]**	***Nephelomys*[3]**	***Tanyuromys*[4]**
Mystacial vibrissae	very long	very long	very long	short (not extending posteriorly beyond pinnae)	short (not extending posteriorly beyond pinnae)	very long
Superciliary vibrissae	very long	very long	very long	short (not extending posteriorly beyond pinnae)	short (not extending posteriorly beyond pinnae)	very long
Tail	unicolored	unicolored	unicolored	distinctly bicolored	distinctly or indistinctly bicolored	unicolored
Ear	small (not extending anteriorly to eye)	small (not extending anteriorly to eye)	large (extending anteriorly to eye)	large (extending anteriorly to eye)	small (not extending anteriorly to eye)	small (not extending anteriorly to eye)
Incisive foramina	short	short	short	short or long	long	short
Interorbit	anteriorly convergent	anteriorly convergent	anteriorly convergent	anteriorly convergent	variable	anteriorly convergent
Jugal	large	large	large	small	small	large
Mastoid capsule	not fenestrated	not fenestrated	fenestrated or not fenestrated	not fenestrated	fenestrated or not fenestrated	not fenestrated
Mesopterygoid fossa	extends between maxillae	extends between maxillae	extends between maxillae	extends between maxillae or not	extends between maxillae and often toothrows	extends between maxillae
Alisphenoid strut	absent	absent	present	usually absent	usually absent	absent
Carotid circulatory	pattern 1	pattern 1	pattern 1	pattern 1	pattern 1	pattern 3
Capsular process	indistinct or absent	indistinct or absent	indistinct or absent	typically present	indistinct or absent	indistinct or absent
M1 anterocone	barely divided	undivided	undivided	undivided	divided	undivided
M2 internal fossette(s)	two	two	usually absent	two	one	one
M1 accessory root	present	absent	present	typically present	absent	present
m1 accessory root	absent	absent	absent	typically absent	present	present
m2 hypoflexus	long	long	long	short	short	long

[1] Data after Brito et al. (2021); [2] Data after Brito et al. (2020); [3] Data after Weksler et al. (2006); [4]Data after Weksler (2015)

al. 2018), is more difficult to differentiate from the Kutukú specimen by tail or vibrissae characteristics. In fact, the marked external resemblance between *Mindomys* and *Tanyuromys* was early highlighted (Hershkovitz 1948:56). However, the two recognized species within this genus, *T. aphrastus* (Harris, 1932) and *T. thomasleei* Timm et al., 2018, show a unique molar occlusal morphology which was described as "…an apomorphic and complex occlusal pattern having extensive, deep, steep-sided flexi and fossettes (enamel islands) with irregular and jagged

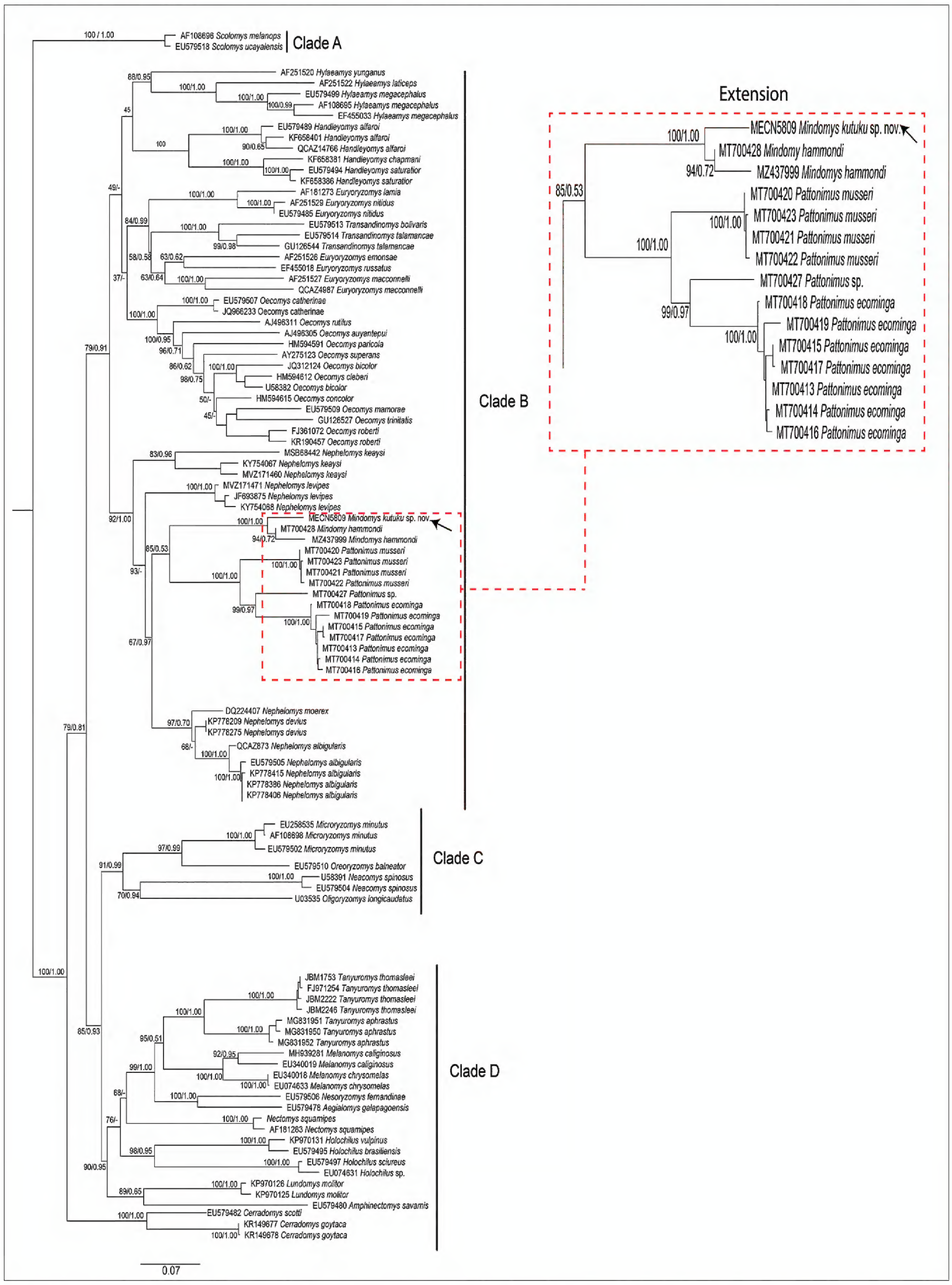

Figure 3. Phylogenetic tree of maximum likelihood of the tribe Oryzomyini based on the Cytochrome b gene. The red box highlights the location of *Mindomys* and *Pattonimus* (magnified on the right), while the arrow indicates the new species here described as *Mindomys kutuku* sp. nov. Letters **A–D.** indicate those clades proposed by Weksler (2006). The values above and below the branches are the bootstrap values and posterior probabilities (BS / PP), respectively.

borders" (Weksler 2015b:455). Although the rodent from Kutukú also has complex molars, several trenchant differences are detected (e.g., absence of irregular and jagged borders, very different overall m1 morphology; Figs 1, 2). In addition, *Tanyuromys* differs from the other genera and the specimen under study in having a carotid circulatory pattern 3 (Table 1).

The phylogenetic result of the IB and ML analyzes presented similar topologies (Fig. 3). The specimen from Kutukú (MECN 5809) was resolved within clade B of the tribe Oryzomyini (Weksler 2006; Brito et al. 2020) together with: ((*Hylaeamys* + *Handleyomys*) + (*Euryoryzomys* + *Transandinomys*) + *Oecomys*)) + (*Nephelomys* + (*Mindomys*): MECN5809 + (MT700428 + MECN6228)) + (*Pattonimus* + *Nephelomys*)). Within the *Mindomys* clade, the Esmeraldas and Carchi specimens, representing *M. hammondi*, were recovered together (PP: 0.75 / BS: 94), while the Kutukú specimen was resolved as sister to the Esmeraldas + Carchi samples (1.00 / 100). Genetic divergences among these samples varied from 3% to 5% (Table 2). The closest phylogenetic genus was *Pattonimus* from the Chocó montane forest (Brito et al. 2020, Table 2).

The data presented above confirmed that we are dealing with an undescribed species of the genus *Mindomys*. We provide below a description for this taxon.

Table 2. Uncorrected genetic distances in percentages (p-distances) between *Mindomys kutuku* sp. nov. (MECN 5809) and the phylogenetically closest species. Distances based on the cytochrome b gene (1140bp). The values on the over diagonal represent the standard deviation.

		1	2	3	4	5
1	*Mindomys kutuku* sp. nov.		0.69	1.21	1.20	1.16
2	*Mindomys hammondi*	3.14		1.06	1.12	0.88
3	*Pattonimus ecominga*	12.50	11.28		1.01	0.86
4	*Pattonimus musseri*	12.11	11.08	7.34		0.98
5	*Pattonimus* sp.	12.72	11.81	7.15	7.24	

Family Cricetidae Fischer, 1817
Subfamily Sigmodontinae Wagner, 1843
Tribe Oryzomyini Vorontsov, 1959
Genus *Mindomys* Weksler, Percequillo & Voss, 2006

***Mindomys kutuku* sp. nov.**

http://zoobank.org/3228B2D2-6F14-4E8C-B82D-EA9FC5992731

Kutukú Rat, Rata de Kutukú

Holotype. MECN 5809 (field number JBM 1849, Fig. 4), an adult male specimen preserved as skull, partial postcranial skeleton, and skin in good condition; collected by Jorge Brito, Jenny Curay and Rubí García on 11 September, 2017.

Type locality. Cordillera de Kutukú (-2.78444°S, -78.140000°W, [coordinates taken by GPS at the trapsite], elevation 1,925 m), Parroquia Patuca, Cantón Méndez, Provincia Morona Santiago, República del Ecuador (Fig. 5).

Diagnosis. A species of *Mindomys* smaller than *M. hammondi*, with opisthodont upper incisors; zygomatic notch very shallow; zygomatic plate moderately narrow and almost without upper free border; zygomatic plate frontally directed; posterior margin of the zygomatic plate anterior to M1; interorbital constriction moderately posterior and narrow; molars of absolute larger size comparatively to the skull, large jugal fully separating maxillary and squamosal portions of the zygomatic arch; hamular process of pterygoid large; alisphenoid strut present; parietal lateral "wing" reaching the zygomatic root; otic capsule medium in size; undefined hamular process of the squamosal; paraoccipital process small; well-exposed petrosal; caudally directed foramen magnum; minute Hill foramen; long incisive foramen; inferior ridge of the masseteric crest not concealing the lower margin of the dentary; lateral view of m3 not hidden by the ascending ramus; angular process of the dentary shorter than condyle; M1 broad, with anterior stylar shelf, anteroposteriorly compressed procingulum and defined anterolingual conule; M1 paracone and metacone transversally compressed; M1 accessory root present; M2 mesofosette rounded; M3 posterior lobe transversally compressed with closed metaflexus.

Morphological description of the holotype. Dorsal fur dark reddish-brown (Fig. 6); flanks similar to dorsum; ventral pelage pale yellow; yellowish and reddish at the edges of the gular region (Fig. 7). Mystacial vibrissae abundant and long, some extending posteriorly beyond shoulder when laid back against cheeks; relatively small but visible pinnae on the fur of the head, naked in appearance but covered with abundant short reddish hairs. Upper side of the front and hind feet abundantly covered with brown hairs, digits covered with short, whitish hairs; the ends are each covered with a few silver hairs which protrude slightly beyond the tip of the claws; ventral surface of manus naked, with five fleshy tubercles (Fig. 8); claws short, recurved, basally opened, except for pollex which bears a nail; pes moderately short and wide, with outer digits (1 and 5) shorter than middle three (claw of d1 extending to start of second phalange of d2, claw of d5 extending to start of second phalange of d4); plantar surface naked with six pads (2 metatarsal and 4 interdigital). Tail long (about 130% of head and body length) and unicolored (dark above and below), covered with long and hirsute hairs, which can extend up to four scales, however the hairs are sparse and give a naked appearance; tip of tail has a 5 mm tuft of hair (Fig. 7).

Cranium with moderately long and wide rostrum (Fig. 4); rostrum barely tapers forward from the nasolacrimal capsules; nasals gradually diverge forward, with the distal end moderately turned upwards; shallow but distinct zygomatic notches; interorbital constriction moderately posterior and narrower; fronto-parietal suture U-shaped; braincase slightly inflated and elongated; cranial roof dorsal profile flat from nasals to the half of parietals to slope gently downward toward the occiput; foramen magnum caudally oriented. Premaxillae slightly shorter than nasals not produced anteriorly beyond incisors, without forming a rostral tube; gnathic process very small;

Figure 4. Three-dimensional reconstruction of the skull of *Mindomys kutuku* sp. nov. based on micro-CT data of the holotype (MECN 5809; Cordillera de Kutukú, Ecuador): cranium in dorsal, ventral, and lateral view, and left hemimandible in labial view. Scale bar: 10 mm.

zygomatic plates moderately narrow and almost without free upper borders; zygomatic arches sturdy and robust; larger jugals; squamosal-alisphenoid groove poorly visible through the translucent braincase, without a perforation where it crosses the depression for the masticatory nerve; small stapedial foramen and carotid canal, but barely expressed petrotympanic fissure; primitive cephalic arterial supply (pattern 1 of Voss 1988); alisphenoid strut present; small anterior opening of alisphenoid canal; postglenoid foramen narrow, subsquamosal fenestra absent and undefined hamular process of squamosal; undeveloped tegmen tympani; parietal "wings" extending to zygomatic roots; small bullae with long stapedial processes; large pars flaccida of tympanic membrane present; orbicular apophysis of malleus well developed; paraoccipital process small. Small Hill foramen; long, pear-shaped incisive foramina, well anterior to the anterior faces of M1; capsular process of premaxillary little developed; palate narrow and short, with the anterior border of the mesopterygoid fossa even with the posterior faces of M3s; posterior palatal foramina small; small paired posterolateral pits located next to the anterior part of the mesopterygoid fossa; broad mesopterygoid fossa, much broader than parapterygoid plates, with V-shaped anterior margin and fully ossified bony roof; massive and projected hamular processes of pterygoids; ventrally well-exposed petrosals.

Mandible robust (Fig. 4), with little-developed falciform coronoid process with its tip at condyle level; laterally placed mental foramen; broad incisor case; scarcely-marked higher masseteric ridge; broad condyle with well-developed pre- and postcondylid processes; alveolus of lower incisor with small capsular process on lateral mandibular surface; poorly excavated lunar notch; short and broad angular process.

Maxillary molar rows large (Fig. 9); main cusps opposites; M1 rectangular and broad; with anterior stylar shelf, anteroposteriorly compressed procingulum and defined anterolingual conule; transversally compressed paracone and metacone; M2 mesofosette rounded; M3 posterior lobe transversally compressed with closed metaflexus. M1 four-rooted (with one accessory labial root); M2 and M3 three-rooted (Suppl. material 3).

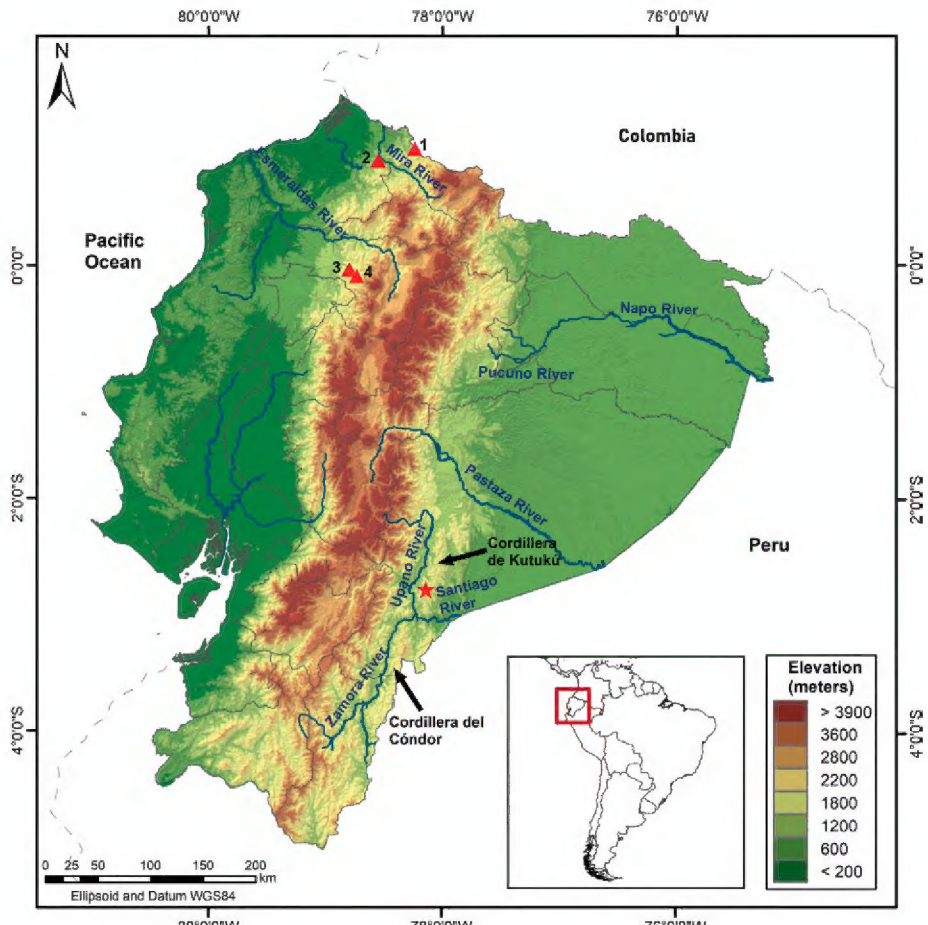

Figure 5. Known recorded localities for *Mindomys hammondi*, Ecuador (in triangles): **1.** Reserva Drácula (Brito et al. 2021); **2.** Alto Tambo, Esmeraldas (Pinto et al. 2018); **3.** Saloya (probably the provenance of the specimen housed at the Museum of Comparative Zoology, Harvard, under the number MCZ 52688); **4.** Mindo (type locality; Thomas 1913); star = Cordillera de Kutukú, type locality of *Mindomys kutuku* sp. nov.

Unusually long and wide flexids in m1-m2; procingulum of m1 not divided into labial and lingual conulids; indistinct anterolophid; mesolophid present; large posterolophid present; wide and deep protoflexid; m2 squared in outline; without internal mesofosette; mesolophid, posterolophid showing the same condition as in m1; m3 sub-triangular in outline with a deep hypoflexid; small entoflexid in line with hypoflexid. Lower molars two-rooted (Suppl. material 3).

Tuberculum of first rib articulates with transverse processes of seventh cervical and first thoracic vertebrae; second and third thoracic vertebra with differentially elongated neural spine; 19 thoracicolumbar vertebrae, the 16–17th with moderately developed anapophyses; 4 sacrals; 38 caudals, with complete hemal arches in the second and third; 12 ribs.

Distribution and remarks. Known only from the type locality (Fig. 5). The zoogeographic terrain in which *M. kutuku* was collected belongs to the eastern subtropics (Albuja et al. 2012). The holotype was collected in evergreen montane forest of the Cordilleras Cóndor-Kutukú (Ministerio del Ambiente del Ecuador 2013), which is characterized by trees with abundant orchids, ferns and bromeliads. The height of the emerging vegetation reaches up to 25 m. *M. kutuku* was collected within a mature forest near a stream (Fig. 10). The surrounding undergrowth has a visual domain of herbaceous families such as Araceae and Melastomataceae. On the slopes, the

Figure 6. External aspect of *Mindomys kutuku* sp. nov., in its natural habitat (painted by Glenda Pozo).

Table 3. External and skull measurements (in mm).

	M. kutuku		*M. hammondi*	
	Holotype MECN 5809	**MECN 6228**	**GNM**	**Holotype NHMUK 13.10.24.58**
Head and body length	151	175	199,5 (188,0–220,0) [4]	203
Tail length	197	236	182,5 (170,0–210,0) [4]	251
Hind foot length (including claw)	32.5	42	40,3 (39,0–42,0) [4]	42
Ear length	18	20	16,6 (15,0–18,7) [4]	18
Length of longest mystacial vibrissae	61.50	78.74	–	–
Length of longest superciliary vibrissae	45.18	51.63	–	–
Length of longest genal vibrissae	27.60	29.90	–	–
Body mass (in grams)	95	184		
Occipitonasal length	35	39.26	43,1 (42,0–45,0) [3]	43
Condylo-incisive length	33.58	36.77	–	39
Length of upper diastema	10.70	10.77	–	12
Crown length of maxillary toothrow	5.95	6.5	–	6.8
Length of incisive foramen	6.16	5.65	–	6.7
Breadth of incisive foramina	2.70	2.52	–	1.86
Breadth of M1	1.86	1.94	–	–
Breadth of rostrum	6.45	8.31	–	–
Length of nasals	12.74	13.80	15,9 (15,4–16,3) [3]	16
Length of palatal bridge	6.92	8.68	–	–
Breadth of bony palate	3.55	3.83	–	–
Least interorbital breadth	5.50	6.48	–	7.7
Zygomatic breadth	18.31	19.63	21,8 (21,0–23,2) [3]	21.5
Breadth of zygomatic plate	3.46	4.39	–	4.6
Lambdoidal breadth	13.60	15.48	–	13.7
Orbital fossa length	12	12.82	–	–
Bular breadth	4.43	4.80	–	–
Length of mandible	18.35	19.66	–	–
Crown length of mandibular toothrow	6.13	6.58	–	–
Length of lower diastema	5.10	4.64	–	–
Length M1	2.74	3.06	–	–
Width M1	1.86	1.94	–	–
Length M2	1.71	2.20	–	–
Width M2	1.79	1.95	–	–
Length M3	1.45	1.51	–	–
Width M3	1.54	1.68	–	–
Length m1	2.64	2.68	–	–
Width m1	1.76	1.88	–	–
Length m2	1.72	1.96	–	–
Width m2	1.70	1.88	–	–
Length m3	1.72	2.05	–	–
Width m3	1.46	1.65	–	–
Source	This study	Brito et al. 2021	Tirira and Högström 2011	Thomas 1913

royal palm (*Dictyocaryum lamarckianun*) predominates. The new species was collected in sympatry with the didelphids *Marmosops caucae* and *Monodelphis adusta* and the sigmodontine rodents *Akodon aerosus*, *Chilomys* sp., *Hyaleamys yunganus*, *Nephelomys auriventer*, *Microryzomys minutus*, *Oecomys superans*, *Oreoryzomys balneator* and *Rhipidomys albujai*.

Etymology. The specific epithet is a noun in apposition after the type locality, Kutukú.

Comparisons. The traits that clearly separate the two species of *Mindomys* are many and varied. Some of these features represent marked differences, such as the shape of the interorbit, the orientation of the foramen magnum (Fig. 11), the occurrence of the alisphenoid strut (Fig. 12), and the differential exposition of the petrosal (Fig. 12). In addition to the characters provided in the diagnosis (see above), the molars comprise one of the anatomical systems where major differences between *M. kutuku* and *M. hammondi* are detected (Table 4).

Discussion

Systematics and biogeography

The paraphyly of *Nephelomys* as obtained based on the Cytb gene was also reported in Tinoco (2015) and Brito et al. (2020). In both cases, the samples of *N. levipes* (Tinoco, 2015; Brito et al. 2020) and *N. keaysi* (Brito et al. 2020), were placed outside of the clade that contained the other species. This result was also found when including another marker (IRBP) and when analysing

Table 4. Main differential craniodental traits between species of the genus *Mindomys* (Oryzomyini, Sigmodontinae).

	Mindomys hammondi	***Mindomys kutuku* sp. nov.**
Tail length % body head length	124%	130%
Nasals anterior tip	Broad	Narrow
Zygomatic notch	Slightly deeper	Very shallow
Molar relative size to skull	Small	Large
Interorbital constriction	Well anterior	Slightly posterior
General morphology of zygomatic plate	Broad, with short upper free border	Narrow, almost without upper free border
Posterior margin of zygomatic plate	Even or posterior to M1	Anterior to M1
Orientation of zygomatic plate	Adpressed to the cranium	More frontally directed
Optic foramen	Rounded	Compressed
Jugal size	Small, overlapping the zygomatic	Large, not overlapping the zygomatic
Pterygoid hamular process	Small	Large
Parietal lateral "wings"	Not reaching zygomatic root	Reaching zygomatic root
Otic capsule	Small	Large
Squamosal hamular process	Defined	Not defined
Paraoccipital process	Large	Small
Hill foramen	Moderate	Minute
Incisive foramina	Very short	Slightly larger
Petrosal exposition	Moderate	Extensive
Alisphenoid strut	Absent	Present
Orientation of foramen magnum	Ventrally	Caudally
Mental foramen	Completely lateral	Partially lateral
Inferior ridge masseteric crest	Concealing inferior margin of dentary	Not concealing inferior margin of dentary
Lateral expression of m3	Hidden by ascending ramus	Not hidden by ascending ramus
Angular process (dentary)	Larger than condyle	Shorter than condyle
M1 proportion	Narrow	Broad
M1 stylar shelf	Absent	Present
Procingulum	Compressed	Not compressed
Anterolingual conule	Undefined	Defined, small
M1 paraflexus	Small, not abruptly shifted	Large, abruptly shifted backwards
M1 mesofosette	Compressed	Rounded
M1 paracone	Broad	Compressed
M1 metacone	Broad	Compressed
M1 accessory root	Absent	Present
M2 paraflexus	Not penetrating to protocone	Penetrating to protocone
M2 paracone	Broad	Compressed
M2 internal mesofosette	Compressed	Rounded
M3 posterior lobe	Developed	Compressed
M3 metaflexus	Open	Closed
M3 paraflexus	Large	Small

both concatenated genes (Cytb + IRBP; see Brito el al. 2020: Fig.2). *N. keysi* and *N. levipes* occupy a range that is disjunct from other species in *Nephelomys* and situated to the south of the depression of Huancabamba in Peru. It is possible that the distance and geographic barriers have isolated these species from the rest of the clade, resulting in evolutionary divergence. We suggest that the genus *Nephelomys* may be made up of two main lineages (north and south) that are reciprocally monophyletic, and that it would benefit from systematic and phylogenetic revision. This review is not the subject of this paper.

Mindomys is among the less-known oryzomyines (Weksler 2006; Weksler et al. 2006; Percequillo 2015b; Brito et al. 2021). Weksler (2006:65), using combined analyses of molecular and morphological evidence, retrieved the genus as the sister group of all other oryzomyines. More recently, Ronez et al. (2021a) found a sister relationship between *M. hammondi* and the extinct Galapagoan *Megaoryzomys curioi* in a morphology-based phylogeny.

Despite being scarcely known, the morphological distinctness of *Mindomys* was highlighted early (Hershkovitz 1944) and promoted its recognition as a separate subgeneric entity (*Macruroryzomys*; a nomen nudum), even under the realm of the evolutionary paradigm in systematic terms (Hershkovitz 1948, 1970). The molecular-based phylogeny advanced here, covering both species of the genus, retrieved *Mindomys* well-nested within clade "B" of Weksler (2006) and sister to *Pattonimus* (Brito et al. 2020, 2021). This hypothesis contradicts the supposed basal position of *Mindomys* (see Weksler 2006) but reinforces its relationship with a group of montane forest oryzomyine genera.

Since the Cordillera de Kutukú belongs to the Amazon Domain, *Mindomys kutuku* constitutes the first undisputed reference for the genus for the eastern side of Ecuador. We said undisputed because there is a previous record from the Oriente region (Museum of Comparative Zoology [MCZ]), but its geographic

Figure 7. *Mindomys kutuku* sp. nov. (MECN 5809, holotype; Cordillera de Kutukú, Ecuador): external aspect based on museum skin in dorsal (**a**), ventral (**b**), and lateral (**c**) view. Scale bar: 50 mm.

Figure 8. Cheiridia appearance in *Mindomys kutuku* sp. nov. (**a, c, e, g** MECN 5809, holotype; Cordillera de Kutukú, Ecuador), and *M. hammondi* (**b, d, f, h** MECN 6228, Reserva Drácula, Ecuador): Right hind foot, plantar view (**a, b**); Right hind foot, dorsal view (**c, d**); Right fore foot, plantar view (**e, f**); Right fore foot, dorsal view (**g, h**). Scale bar: 10 mm.

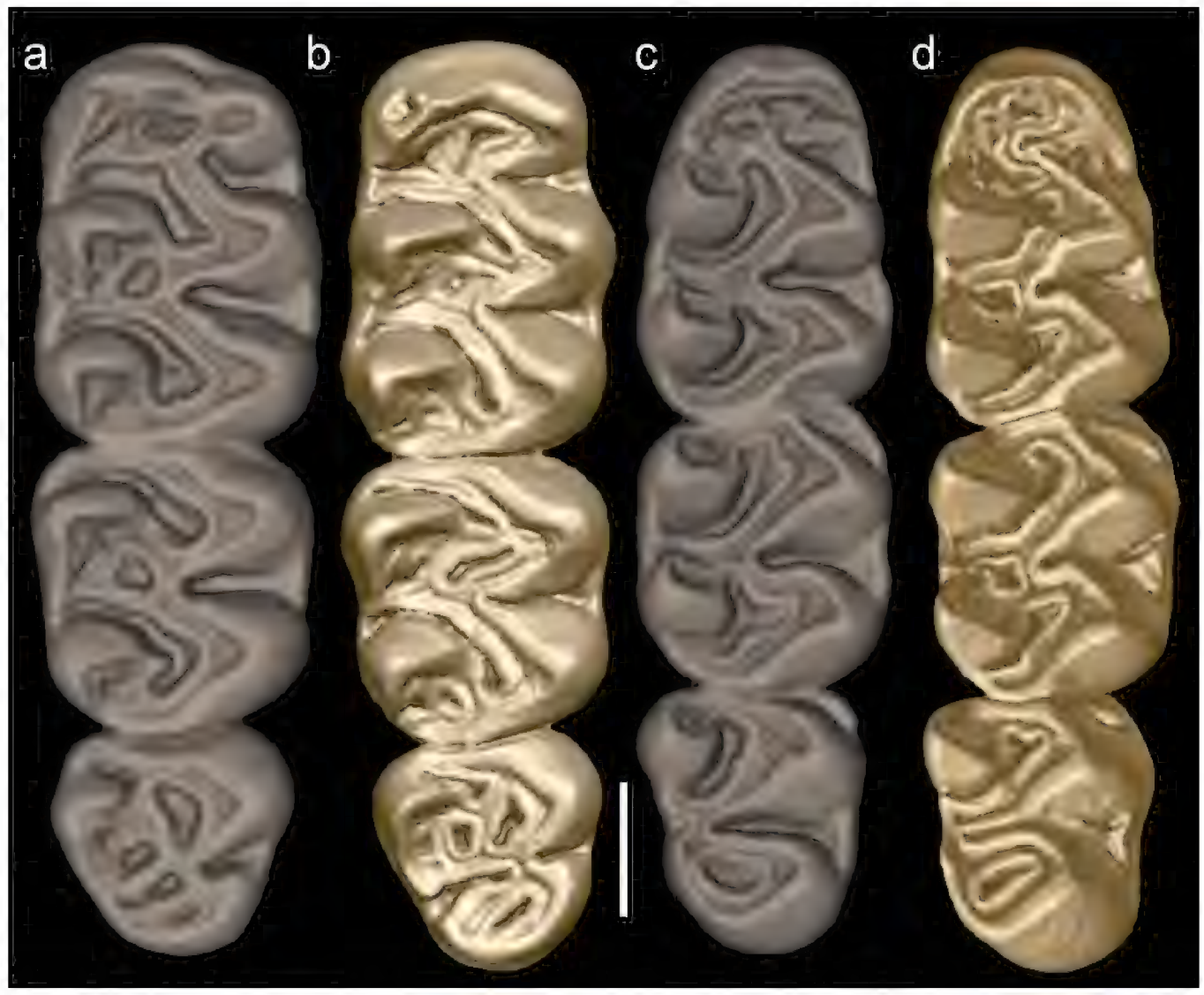

Figure 9. Three-dimensional reconstructions of the occlusal view of right upper (**a, b**) and lower (**c, d**) toothrows based on micro-CT data of the holotypes of *Mindomys kutuku* sp. nov. (**a, c** MECN 5809; Cordillera de Kutukú, Ecuador) and *Mindomys hammondi* (**b, d** NHMUK 13.10.24.58; Mindo, Ecuador). Scale bar: 1 mm.

provenance (originally recorded as Napo, Concepción) was questioned (Weksler et al. 2006:16; McCain et al. 2007:135). This specimen was collected by R. C. Olalla & sons on 27 July, 1929, and entered to the museum as part of a large sample of Amazonian mammals (including sciurids, chiropterans, caviomorphs, primates, and also other cricetids such as *Hylaeamys*, *Oecomys*, etc.). However, the specimen is actually composed of parts of two different animals (skull, MCZ 52543 = *Mindomys*; skin, MCZ 52688 = *Proechimys*). These animal parts were apparently mixed up by the collectors and the numbers were switched, as already detected by Charles Handley (on the specimen label). A second collection locality associated with these materials was recorded as "Chaloya, Mindo, Occidente, Ecuador" by the collectors (on the label). Although there is no place called Chaloya near Mindo (Paynter 1993), 5 km west to the latter is Saloya, a small town perched on the east margin of the homonymous river. Probably, the forests around Saloya are the real provenance of the MCZ 52543, a full adult *Mindomys* morphologically inseparable from *hammondi*.

External morphology and arboreality in sigmodontines

Arboreality has long been suspected of *Mindomys*. Hershkovitz (1970:793) stated that "*hammondi*… is an extremely long-tailed, broad-footed rat modified for arboreal life." The pes in *Mindomys* was described as short and broad (Hershkovitz 1944:82). In addition, Thomas (1913:570) noted: "fifth hind toe, without claw, reaching to the end of the first phalanx of the fourth;" therefore, a moderately long digit. Apparently, some controversy exists regarding the length of the hind foot (including claw) in the holotype of *M. hammondi*, with "successive" values of 32 mm (Thomas 1913), 32 mm, 41 mm, and 42 mm (see Hershkovitz 1970:table 2 for a detailed indication of when these measurements were recorded). Additional specimens attributed to the species have measured 41 or 42 mm (Hershkovitz 1970), although Percequillo (2015b) stated that the pes ranged between 38 and 42 mm. For the holotype, Thomas (1913:571) recorded a tail length equal to 251 mm versus a head and body length equal to 203 mm. Based on a larger series, Percequillo (2015b:360), described *M. hammondi* as having a head and body length between 173– 293 mm and with a tail much longer than head and body (tail length = 222– 251 mm). Until now, no other observations, based on dry skins, support arboreality in *Mindomys*.

Arboreality is the least studied mode of life in the entire sigmodontine radiation. Most of the limited research conducted was based on quantitative and, more rarely, qualitative osteological postcranial features (e.g., Carrizo and Díaz 2011, 2013; Coutinho et al. 2013; Carrizo et al. 2014; Coutinho and Oliveira 2017; Tavares et al. 2021). From external anatomy, the main contribution that addressed arboreality was the revision of *Oecomys* (Hershkovitz 1960). Hershkovitz (1960) discussed relative size and geometry of pes, plantar pads, pes claws, and relative tail length and pilosity as arboreal adaptations. A moderately short and broad hind

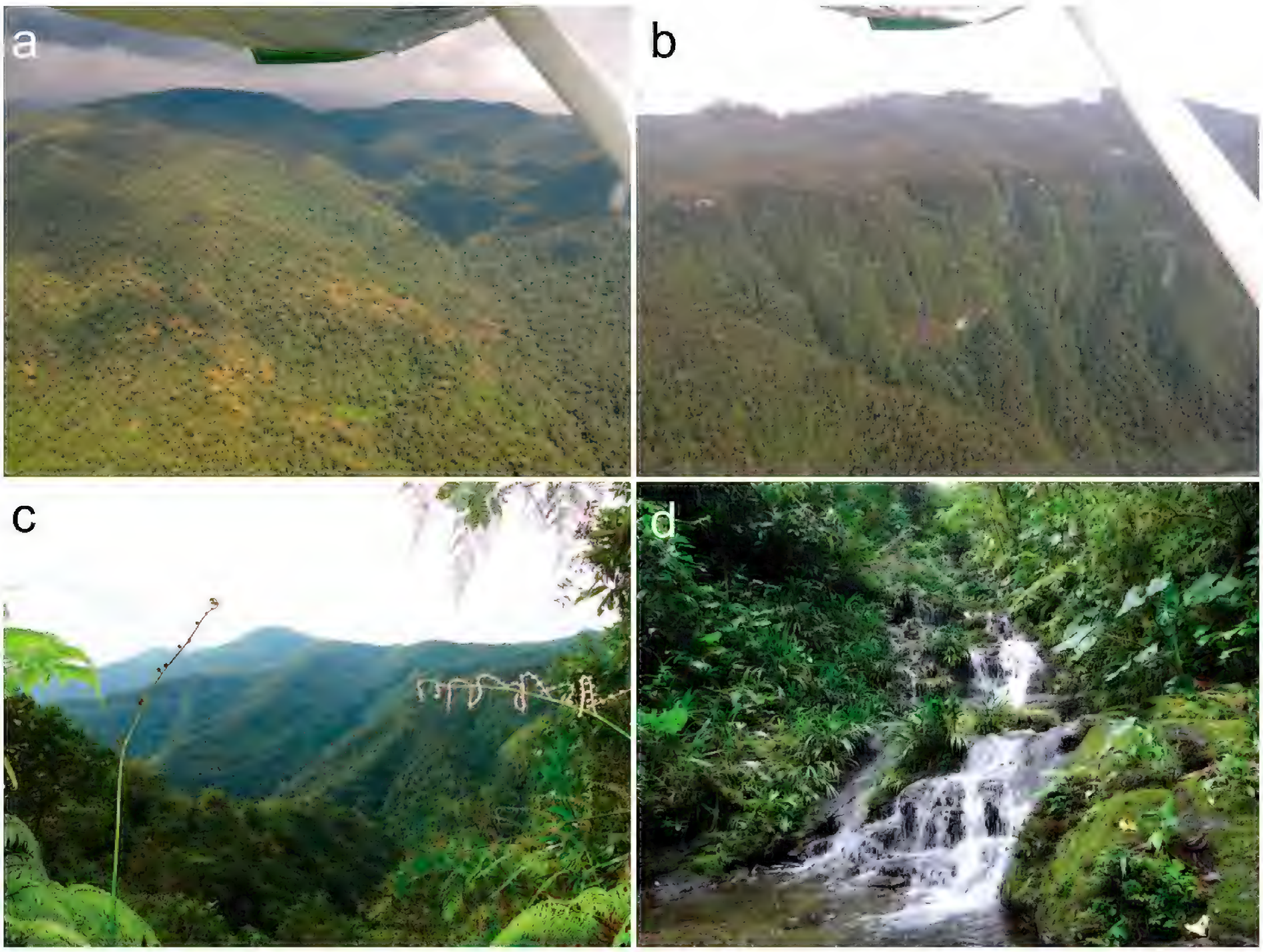

Figure 10. General landscape of the Cordillera de Kutukú (Ecuador), aerial survey in east-west orientation (**a, b**), photographs taken on August 26, 2017; field expedition in evergreen montane forest (**c, d**), and stream near the trapping site (**d**), photographs taken on September 8, 2017.

foot was considered as reflecting arboreality while a long and narrow hind foot was regarded to be associated to cursoriality (Hershkovitz 1960:525). Plantar pads "large and with little space between them" were also highlighted as potentially useful to clutch "slender branches and twigs… between apposing tubercles" (Hershkovitz 1960:525). Claws "thick, comparatively short, recurved… [with] tips sharp and raised well above the ends of the toes" were considered unsuitable for digging or grasping activities and, therefore, associated to arboreal life (Hershkovitz 1960:525). Although the tail in *Oecomys* was not recognized as "a specialized tool for arboreal life… [because it] is not remarkably long" (Hershkovitz 1960:525), he noted that "in arboreal, saltatorial and some aquatic cricetines, the tail has become longer, at least on an average" (Hershkovitz 1960: 526–527). In addition, tail hairiness, especially the length of hair on the caudal apex, was noted as well-expressed in arboreal cricetids and probably associated with sensory functions. Hershkovitz (1969:42) summarized: "Arboreal oryzomyines… have long semi-prehensile tails covered, at least terminally, with long tactile hairs. Their feet are broad, with long and partially opposable outer digits, recurved claws, and enlarged plantar tubercles adapted for clutching slender branches and twigs." Rivas-Rodríguez et al. (2010) highlighted that certain arboreal and scansorial sigmodontines have numerous larger and, in the case of *Rhipidomys*, thicker mystacial vibrissae. They also remarked on the differential size of palmar pads in *Oecomys* and *Rhipidomys* (Rivas-Rodríguez et al. 2010: fig. 2), a trait not previously recorded in a comparative context, as well as the greater development of both plantar pads and the length of the fifth pedal digit, the occurrence of enlarged and pointed pedal claws (see also Rivas and Linares 2006), and lengthy, well-haired and apical stuffed tails (Rivas-Rodríguez et al. 2010: 101–102). Short, high, and sharply curved pedal claws were listed as key features associated to climbing activities in the scansorial *Oligoryzomys*; more indeed, Tulli et al. (2016:88) concluded that "claw height and curvature may be considered genuine traits, allowing organisms to occupy an arboreal niche, because this feature is likely related to an increase in frictional grip on arboreal substrates."

A large body of evidence shows that those presumed arboreal sigmodontines have long tails, whereas the opposite is true in fossorial forms. According to Carrizo et al. (2014), long tails, those with a number of caudal vertebrae between 36 and 40, characterize climbing genera (*Irenomys*, *Juliomys*, *Oligoryzomys*, and *Rhipidomys*). Furthermore, these authors stated "The elongate tails of

Figure 11. Three-dimensional reconstructions of selected aspects of qualitative anatomy contrasted in the crania (dorsal view to the left, ventral view to the right) based on micro-CT data of the holotypes of *Mindomys kutuku* sp. nov. (left; MECN 5809; Cordillera de Kutukú, Ecuador) and *Mindomys hammondi* (right; NHMUK 13.10.24.58; Mindo, Ecuador), scaled to the same length. The figure portrays differences between the characteristics of these species as follows: *M. kutuku* sp. nov. has shallower zygomatic notch (zn), posteriorly displaced interorbital constriction (ic), longer incisive foramina (if), larger molars (m), larger auditory bulla (ab), and more caudally directed foramen magnum. Figures are not to scale to facilitate comparisons.

these taxa would similarly seem to represent convergent traits related to balance… The prehensile tail of *Rhipidomys* may possibly have arisen independently from that of *Irenomys* and *Juliomys*" (Carrizo et al. 2014:475). In agreement with what was recorded for the holotype of *M. hammondi*, *M. kutuku* has a tail that surpasses the head and body length by about 50 mm (Table 3). We can conclude that both species are long-tailed rats. The tail of *M. hammondi* is covered by long hairs partially hidden by caudal scales (Percequillo 2015b:360). *M. kutuku* shows a similar condition in tail pilosity, adding a caudal apical tuft of about 5 mm. The number of caudal vertebrae in both species of *Mindomys* is similar, 35 for an adult *M. hammondi* (Brito et al. 2021) and 38 for the holotype of *M. kutuku*. Therefore, these species of *Mindomys* can be considered "arboreal" when judged by tail length. However, no studies have been specifically conducted to test tail functionality in sigmodontines, or to explore the almost certain direct correlation between tail length and body size. Most of our ideas about tail properties in those sigmodontines treated as "climbers" are mirrored from much better studied groups of rodents, such as squirrels, and also other comparatively well-known arboreal mammals (e.g., marsupials). Accordingly, the characterization of some sigmodontines as having prehensile tails (Hershkovitz 1969; Carrizo et al. 2014) is based on little specific evidence, since this has not been tested in any anatomical or controlled behavioral study (see also Nations et al. 2019:332).

Beyond measurements and general pilosity based on inspection of dry skins (Percequillo, 2015b), nothing is known about the cheiridia of *Mindomys*. There are four main aspects of the hind feet of *Mindomys* that require attention in relation to its potential arboreal specialization: overall geometry and aspect, general size and digits length, pads features, and claws morphology. The specimen of *M. kutuku* offers the opportunity to examine these issues with some detail. It has a broad and short hind foot, with proportionately short and thick digits. The basal portion of the digits is covered with granules, being medially clearly ringed and distally having patent calluses. The latter are so bulging that the claws are clearly separeted from the basal plane. The hind feet comprise 21.5% of the body-head length (the same value is recorded for the holotype of *M. hammondi*). The plantar surface is naked, smooth, pinkish colored, has no squamae except a few granules and is crossed by a system of delicate striae. The pad complement is composed of six elements, being almost equal in size, bulbous and turgent. The hypothenar is the largest one and the third digit pad is the smallest. The interspace enclosed by the pads is enough to contain the hypothenar pad. The claws are short, moderately pointed, basally open, and dorsally covered by sparse ungual tufts that barely reach the ends; digit I almost lacks ridges and

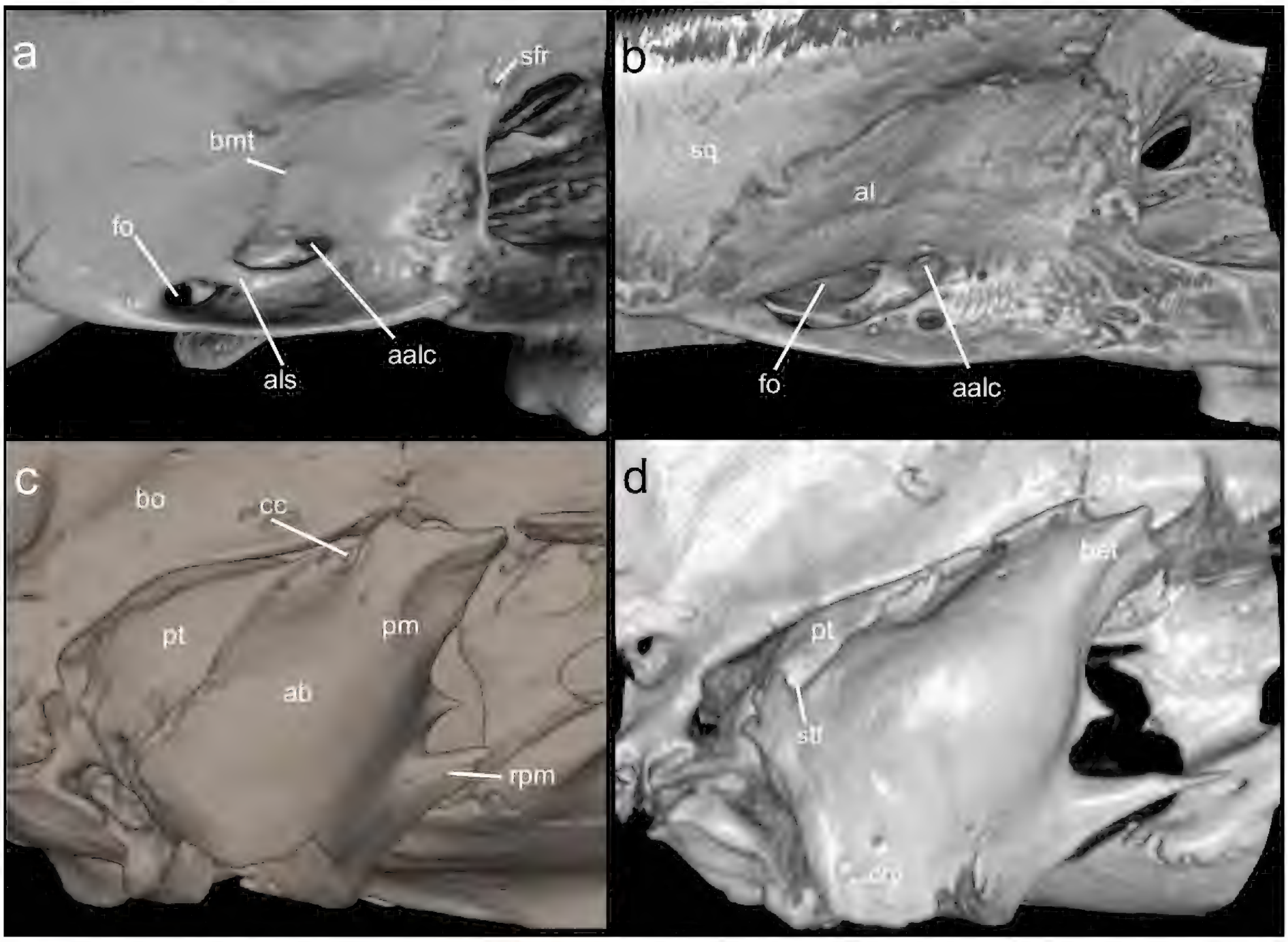

Figure 12. Three-dimensional reconstructions of details of the alisphenoid region (**a, b**) and the auditory bulla (**c, d**) based on micro-CT data of the holotypes of *Mindomys kutuku* sp. nov. (**a, c** MECN 5809; Cordillera de Kutukú, Ecuador) and *Mindomys hammondi* (**b, d** NHMUK 13.10.24.58; Mindo, Ecuador). Acronyms: aalc, anterior opening of alisphenoid canal; ab, auditory bulla; al, alisphenoid; als, alisphenoid strut; bet, bony Eustachian tube; bo, basioccipital; cc, carotid canal, cty, crista tympanica; fo, foramen ovale; bmt, buccinators-masticatory trough; pt, petrosal; sfr, sphenofrontal foramen; sq, squamosal; stf, stapedial foramen; rpm, rostral process of malleus. Figures are not to scale to facilitate comparisons.

ungual tufts; digits II to IV are the largest and subequal in length; digits I and V are slightly shorter with respect to the central digits. Are these described features sufficient to support arboreality in *M. kutuku*? Certainly not. However, a visual comparison with the hind foot in other sigmodontines suggests a unique, "intermediate" morphology for the species (Suppl. material 5). Evidently, *M. kutuku* does not have the strikingly broad and short pes that characterize several arboreal or climbing sigmodontines (e.g. *Juliomys*, *Rhagomys*), but neither the narrow, long-fingered, and inconspicuously padded pes of comparable cursorial oryzomyines (e.g., *Nephelomys*). An aspect pending study in sigmodontines is the histology of the fleshy pads, particularly in relation to the existence and position of glands for the production of adhesive substances or moistening (Haffner 1998).

Probably the manus is one of the less explored complex anatomical systems in sigmodontines, in which arboreality is decidedly expressed (Camargo et al. 2012; Nations et al. 2019). Among the scarce assessments of sigmodontine manus are the description provided by Luna and Patterson (2003) for the arboreal *Rhagomys longilingua* and the approach of Miljutin (2010) on *Megalomys desmarestii*, favoring a cursorial life-mode for this giant oryzomyine (contra Hershkovitz 1969:42). *M. kutuku* has a broad manus with thick digits. The palmar surface is naked, granulose and almost entirely occupied by five fleshy pads, with the metacarpals slightly larger than the carpals. The narrow space enclosed by the carpal pads is crossed by a longitudinal groove. The digits are finely ringed and end distally in turgent calluses, showing the same condition as described for the pedal calluses. The claws are short, recurved, pointed, and basally opened, and are barely covered by scarce ungual tufts. The digits II to IV are subequal in length; the digit V is slightly shorter. Digit I has a nail instead of a claw and lacks ungual tufts. As was noted above for the pes, the manus in *M. kutuku* seems to represent a morphological "intermediate degree" between typical arboreal or scansorial sigmodontines and cursorial forms (Suppl. material 5). In contrast, *M. kutuku* has significantly more developed metatarsal pads, almost without space in between.

It is intriguing why sigmodontine manus are markedly less explored than pes. In the extensive revision of anatomical attributes conducted by Weksler (2006:105), just six traits (five external and one osteological) were

compiled from previous literature to describe the manus. Since two of these features refer to the claws, and one to the ungual tufts, it is clear that manus was mostly neglected by operational limitations, not by informative power. If the morphology of the manus is assessed directly on dry skins, without moistening (contrary to what P. Hershkovitz regularly did), almost nothing can be surmised from the palmar anatomy beyond sole condition. Even when working with fluid-preserved specimens, or more rarely with recently dead animals, manus received little attention, and few reports recorded their main features (e.g., Hershkovitz 1966, 1994, 1998; Hinojosa et al. 1987; Miljutin 2010; Pardiñas et al. 2016).

Other external features, beyond those discussed previously, have been tentatively connected as adaptations to arboreal life in sigmodontines. Pine (1980:199) highlighted the bicolored condition of the feet of *Juliomys pictipes* and remarked "this feature implies arboreal habits to me. It is a curious thing that small arboreal rodents tend to have pale toes and dark middorsal patches on the hind feet… Other characteristics which seem to be correlated with arboreal life… are: immaculate white bellies and perhaps dark rings around the eyes and pale gray or bright reddish dorsal coloration." Head vibrissae, in particular the number, length, and rigidity, have also been vaguely associated with arboreality (Tribe 1996; Rivas-Rodríguez et al. 2010). Coloration and whiskers remain unstudied.

Concluding remarks

If all species of the genera *Oecomys* and *Rhipidomys* are typified as arboreal, adding the remainder sigmodontines showing moderate to confident adaptations to this mode of life (i.e., *Irenomys*, *Juliomys*, *Mindomys*, *Phaenomys*, *Rhagomys*, *Sooretamys*, and *Wiedomys*), we reach over the 10% of the entire radiation (53 out of 450 species; numbers after Pardiñas et al. 2017). This prompts the question why these rodents have been so poorly successful exploiting this niche? The problem is not trivial beyond the natural limitations associated to explain negative results. Even after 500 years of deforestation, South and Central America and the Caribbean are covered by 834 million hectares of tropical forest and 130 million hectares of other forests, representing nearly one-quarter of the world's forest cover (Nix 2020). To explore why a recent rodent radiation failed to exploit the vertical habitat under these conditions could be valuable to understand several crucial aspects of its evolutionary history. In fact, one of the most candent topics about sigmodontine origins is probably related with the role of the dense forests covering Central America during the Late Miocene (Webb 2006; Woodburne 2010).

The low number of arboreal species in sigmodontines is probably based on numerous factors. Intrinsic characteristics of the members of this subfamily acting as limitations seem possible to discard, since the very similar Tylomyinae, apparently sister to Sigmodontinae, is entirely constituted by arboreal forms (Pardiñas et al. 2017). Prima facie, the "niche saturation" appears as the best working hypothesis to explain the overall lack of arboreality in sigmodontines. Current Tropical American canopies are largely dominated by marsupials, primates, and groups of non-cricetid rodents (e.g., sciurids, echymyids; Hershkovitz 1969; Emmons and Feer 1997; Voss et al. 2001). The knowledge of these groups of mammals during the Late Miocene, when the first sigmodontines are recorded (Ronez et al. 2021b; Prevosti et al. 2021), is still poor; in fact, sciurids are entirely unknown in the South American paleontological record (A. Mones, pers. comm.). However, although based on fragmentary pieces of information, the prior occupancy of forests by marsupials, primates, caviomorphs, and sciurids is beyond doubt (Kay et al. 1997; Pascual 2006; Abreu-Jr et al. 2020). Most likely, Mio-Pliocene sigmodontines repeatedly encountered some kind of forest niche saturation. By contrast, *Araucaria* and *Nothofagus* forests covering the southern Andean foothills are virtually free of canopy mammals (Pearson 1983) including arboreal cricetids (Pardiñas et al. 2015), with the possible exception of *Irenomys* (Amico and Aizen 2000).

The above discussion of arboreality in sigmodontine rodents contains an important message: the need to increase the knowledge of external anatomical aspects. The accurate record of these features implies a change rooted in curatorial practices, including preserving a substantive proportion of animals in fluids, instead of the classical dry skin plus skeleton preparation. In addition, fresh (i.e., recently dead) specimens should be regularly photographed in the field in order to depict in detail those structures that are poorly preserved in typical dry skins (e.g., rhinaria, ears, soles, mammae). The need to gather basic anatomical data runs in parallel with other aspects of knowledge in sigmodontine rodents (e.g., de la Sancha et al. 2017). Fortunately, a new "wave" of fine anatomical exploration is growing in other muroids (e.g., Martinez et al. 2018; Kerbis Peterhans et al. 2020; Wible and Shelley 2020) and will trigger comparable studies in New World cricetids.

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hammondi from Göteborg Naturhistoriska Musset, and José Martínez provided photographs of *E. macconnelli*; the same was done by Alexandre Percequillo and M. Pinto regarding the holotype of *M. hammondi* and one individual from Esmeraldas, respectively. To reach the MCZ specimens during pandemic times we counted with the help and advice of Hopi E. Hoekstra and, in particular, Mark Omura; in addition, Robert M. Timm, who has the MCZ 52543 on loan, kindly shared with us several pictures of this specimen taken by Maria Eifler. After a free critical reading, Marcelo Weksler enriched the manuscript with valuable comments. Néstor Cazzaniga guided us through a 30 minutes tutorial regarding nomenclatorial rules of national adjectives. Érika Cuéllar Soto and Reed Ojala-Barbour helped in linguistic and compositional topics. James Patton illuminates us about Charles Handley initials. Mateo Vega kindly made figure 5. Glenda Pozo "bring to life" the new rodent described here (figure 6) with her characteristic attention to anatomical details and artistic talent. The Ministry of Environment of Ecuador granted the respective research permits: No. 007-IC-DPAMS-MAE-2016 and MAE-DNB-CM-2019-0126. Finally, study travels of UFJP to Quito were funded by Fundación Ecominga and by Javier Robayo. We are deeply indebted to these colleagues and the several institutions mentioned above, but the authors bear the final responsibility for content and organization. This is an Initiative Vorontsov 2030's contribution # 2.

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Appendix 1

Studied specimens belong to the following mammal collections: GNM, Göteborg Naturhistoriska Musset, Gothenburg, Sweden; MECN, Instituto Nacional de Biodiversidad, Quito, Ecuador; MEPN, Museo de la Escuela Politécnica Nacional, Quito, Ecuador; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MUSM, Museo Universidad San Marcos, Lima, Perú; NHMUK, The Natural History Museum, London, UK; and ROM, Royal Ontario Museum, Toronto, Canada. Specimens marked with an * are holotypes of the respective species and those with ** were examined through digital pictures or 3D-scans.

Euryoryzomys macconnelli Thomas, 1910 (n = 1): Perú, Amazonas, El Cenepa (MUSM 27054**).

Hylaeamys yunganus (Thomas, 1902) (n = 8): Ecuador, Morona Santiago, Cordillera de Kurukú (MECN 5805, 5834–36, 5848–51).

Juliomys pictipes (Osgood, 1933) (n = 1): Argentina, Misiones, Reserva Privada "Valle del Arroyo Cuña Pirú" (MLP 1.I.03.24).

Mindomys hammondi (Thomas, 1913) (n = 9): Ecuador, Pichincha, San Miguel de los Bancos, Mindo (NHMUK 13.10.24.58*, GNM 17702-06**); Mindo, Saloya? (MCZ 52543**); Esmeraldas, Alto Tambo (ROM 105820**); Carchi, Reserva Drácula (MECN 6228).

Mindomys kutuku sp. nov. (n = 1): Ecuador, Morona Santiago, Méndez, Cordillera de Kutukú (MECN 5809*).

Nephelomys albigularis (Tomes, 1860) (n = 24): Ecuador, Bolívar, Quebrada de Pistud (MECN 527-28); Cruz de Liso (MECN 578-83); El Oro, Zaruma, Chivaturco (MECN 4782, 4784-99, 4803-04; Chilla, Chilla Cocha (MECN 4813, 4817, 4823-25, 4833-34).

Nephelomys auriventer Thomas, 1899 (n = 5): Ecuador, Morona Santiago, Morona, Sardinayacu (MECN 3797); Mendez, Kutukú (MECN 5812, 5813, 5816); Logroño, Yapit (MEPN 12214).

Nephelomys nimbosus (Anthony, 1926) (n = 6): Ecuador, Morona Santigo, Guabisai (MECN 4323-24); Tinguichaca (MECN 3803); Sambalán (MECN 4325); Tungurahua, Baños, Cerro Candelaria (MECN 5010); Río Cristal (MECN 6090).

Nephelomys moerex (Thomas, 1914) (n = 26): Ecuador, Cotopaxi, Otonga (MECN 1084, 1086); Pichincha, Reserva Pahuma (MECN 2480, 2485, 2513, 2515, 2516-17); Reserva Verdecocha (MECN 2538-39, 2541, 2592); Reserva Maquipucuna (MECN 2545, 2605); Reserva Bellavista (MECN 2816-20, 2824, 2826-30, 2832, 2835).

Oecomys bicolor (Tomes, 1860) (n = 8): Ecuador, Morona Santiago, Cordillera de Kutukú (MECN 5807, 5811, 5814); Parque Nacional Sangay (MECN 4193, 4196, 4242); Zamora Chinchipe, Tundayme (MECN 6116, 6118).

Oecomys superans Thomas, 1911 (n = 4): Ecuador, Morona Santiago, Cordillera de Kutukú (MECN 5807); Orellana, Coca (MECN 2386); Sucumbíos, Río Bermejo (MECN 3360); Putumayo (MECN 3371).

Pattonimus ecominga Brito, Koch, Percequillo, Tinoco, Weksler, Pinto & Pardiñas, 2020 (n = 1): Ecuador, Carchi, Reserva Drácula (MECN 5928*).

Rhagomys septentrionalis Moreno Cárdenas, Tinoco, Albuja & Patterson, 2021 (n = 2): Ecuador, Zamora Chinchipe, Cordillera del Cóndor (MEPN 10898); Morona Santiago, Parque Nacional Sangay (MECN 6172).

Rhipidomys leucodactylus (Tschudi, 1845) (n = 4): Ecuador, Morona Santiago, Parque Nacional Sangay (MECN 4245, 5688, 5868); Tungurahua, Baños (MECN 6131).

Sigmodontomys alfari Allen, 1897 (n = 2): Ecuador, Carchi, Reserva Drácula (MECN 6021, MECN 6022).

Tanyuromys thomasleei Timm, Pine, & Hanson, 2018 (n = 4): Ecuador, Carchi, Reserva Drácula (MECN 4740, 5938); Imbabura, Reserva Manduriacu (MEPN 12606); Pichincha, La Titania (MECN 3407).

Thomasomys aureus (Tomes, 1860) (n = 1): Ecuador, Carchi, Bosque de Polylepis (MECN 3729).

Supplementary material 1

GenBank access numbers of cricetid taxa used in the phylogenetic analyses

Authors: Jorge Brito, Claudia Koch, Nicolás Tinoco, Ulyses F. J. Pardiñas

Data type: GenBank access numbers

Explanation note: Sequences used for phylogenetic analyses.

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Supplementary material 2

Diagnostic traits of *Mindomys* (after Weksler et al. 2006)

Authors: Jorge Brito, Claudia Koch, Nicolás Tinoco, Ulyses F. J. Pardiñas

Data type: Morphological comparison

Explanation note: Diagnostic differences compared to *Euryoryzomys* spp, *Nephelomys* spp., and *Tanyuromys*.

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Supplementary material 3

Figure S1

Authors: Jorge Brito, Claudia Koch, Nicolás Tinoco, Ulyses F. J. Pardiñas

Data type: Morphological comparison

Explanation note: Selected structures compared: Left upper (left panel) and lower (right panel) molar roots in several oryzomyine: *Mindomys kutuku* sp. nov. (A, B; MECN 5809, holotype), *M. hammondi* (C, D; NHMUK 13.10.24.58, holotype), *Nephelomys auriventer* (E, F; MECN 5812), *Tanyuromys thomasleei* (G, H; MECN 3407), and *Sigmodontomys alfari* (I, J; MECN 6021)

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Supplementary material 4

Figure S2

Authors: Jorge Brito, Claudia Koch, Nicolás Tinoco, Ulyses F. J. Pardiñas

Data type: Morphological comparison

Explanation note: Selected structures compared: Lateral views of crania (left panel) and left hemimandibles (right panel) in several oryzomyines: *Mindomys kutuku* sp. nov. (a; MECN 5809, holotype), *Mindomys hammondi* (b; NHMUK 13.10.24.58, holotype), *Nephelomys auriventer* (c; MECN 5812), *Tanyuromys thomasleei* (d; MECN 3407), and *Sigmodontomys alfari* (e; MECN 6021). The jugal and the parietal were masked in light blue and green, respectively

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Supplementary material 5

Figure S3

Authors: Jorge Brito, Claudia Koch, Nicolás Tinoco, Ulyses F. J. Pardiñas

Data type: Morphological comparison

Explanation note: Selected structures compared: Plantar views of right hind feet from adults in several sigmodontines including those typically considered arboreal (upper row): *Oecomys bicolor* (a; MECN 5814), *Rhagomys* sp. (b; MECN 6172), *Juliomys pictipes* (c; MLP 1.I.03.24), *Thomasomys aureus* (d; MECN 3729), *Rhipidomys leucodactylus* (e; MECN 5868), *Mindomys kutuku* sp. nov. (f; MECN 5809), *Pattonimus ecominga* (g; MECN 5928), *Nephelomys auriventer* (h; MECN 5813), *Hylaeamys yunganus* (i; MECN 5805), *Sigmodontomys alfari* (j; MECN 6021). Figures are not to scale to facilitate comparisons

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Supplementary material 6

Figure S4

Authors: Jorge Brito, Claudia Koch, Nicolás Tinoco, Ulyses F. J. Pardiñas

Data type: Morphological comparison

Explanation note: Selected structures compared: Plantar views of right fore feet from adults in several sigmodontines including those typically considered arboreal (upper row): *Oecomys bicolor* (a; MECN 5814), *Rhagomys* sp. (b; MECN 6172), *Juliomys pictipes* (c; MLP 1.I.03.24), *Thomasomys aureus* (d; MECN 3729), *Rhipidomys leucodactylus* (e; MECN 5868), *Mindomys kutuku* sp. nov. (f; MECN 5809), *Pattonimus ecominga* (g; MECN 5928), *Nephelomys auriventer* (h; MECN 5813), *Hylaeamys yunganus* (i; MECN 5805), *Sigmodontomys alfari* (j; MECN 6021). Figures are not to scale to facilitate comparisons

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